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Research Article

Rapid colonisation of a newly formed lake by zebra mussels and factors affecting juvenile settlement

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Abstract

Invasive non-native species are widespread in freshwaters but their capacity to establish in new lakes has seldom been assessed. In this four-year study (2006–2009), we used Side-scan Sonar and underwater video to illustrate how a 200 ha urban, amenity lake at Cardiff Bay (Wales, UK) was invaded extensively by zebra mussels *Dreissena polymorpha* (Pallas) within 2–3 years of creation in 2001. Veliger surveys and artificial substrates were used to assess conditions affecting juvenile settlement. Within 5–8 years of lake formation, all hard substrates at 0.5–7 m held mussel densities of 250–6600 m^{-2} which, coupled with a crude estimate of habitat available, suggested a lake-wide population of at least 9–31 million adults. Veligers reached 8 (± 2 SE) to 14 (± 4) L^{-1} during May–September when water temperatures were >14 °C, but densities and juvenile settlement declined at high discharge when lake flushing rates increased: settled densities in a drier year (2007) exceeded those in a wet year (2008) by 120× implying more effective colonisation under low flows and longer residence times. These data illustrate how rapid invasion by non-native species should be appropriately factored into planning and risk assessments for new water bodies, and potential effects on amenity, ecosystem processes and ecosystem services considered. Our data suggest that drought and low flow under future climates could be a particular risk factor affecting *Dreissena* colonisation.

Key words: Amenity lakes, aquatic, colonisation, *Dreissena*, invasive species, population

Introduction

Invasive non-native species are now so widespread in freshwaters that the organisms involved and ecosystems effects are increasingly predictable (Nichols 1996; Ram et al. 1996; Strayer 2010; Karatayev et al. 2015). In the case of new lakes, however, the risks of invasion and establishment by non-native species have seldom been appraised. Such lakes are created increasingly for water supply, irrigation, flood storage, extractive industries, aquaculture, hydropower or amenity and two features are important. First, new lakes offer a valuable opportunity to assess the rapidity and extent with which invasive species' populations can establish because the starting conditions are known (cf Lucy 2006). Second, invasive species in such locations have the potential for large effects on resource values because new lakes are usually created to deliver specific amenities or ecosystem services. Where the invaders change ecological conditions substantially—as is often the case in zebra mussel *Dreissena polymorpha*—the intended benefits of lake creation could be disrupted.

Zebra mussels are native to the Caspian and Black Seas, but first occurred in Western Europe during the 19th century (Morton 1969; Müller et al. 2002). They have been in Great Britain since 1824 (Sowerby 1825; Morton 1969) and by the 1970s zebra mussels occurred here extensively (Morton 1969). Densities increased further during 1980–2000, when mussels also spread into Ireland (Aldridge et al. 2004), across Europe and into North America (Nalepa et al. 1996; Nichols 1996; Müller et al. 2002). This expansion has since continued (Wong and Gerstenberger 2015).

The ecological and economic impacts of zebra mussels are well described (Stanczykowska and Lewandowski 1993; Nalepa et al. 1995; Nichols 1996). They include changes in lake food webs through the selective removal of phytoplankton (Fahnenstiel et al. 1995), modification of lake biogeochemistry (Effler et al. 1996; Effler and Siegfried

1998), effects on native organisms (Schloesser et al. 1996), fouling of natural or artificial structures and obstruction of water treatment facilities or industrial infrastructure (Ram and McMahon 1996). Assessments of population density, distribution, dynamics, colonization patterns and, ultimately, total population size are therefore essential in understanding the potential impact of zebra mussels when any newly formed lake is invaded (Naddafi et al. 2010). Zebra mussels can colonise almost any hard substrates, more rarely occupying macrophytes (Stanczykowska and Lewandowski 1993; Folino-Rorem et al. 2006) or fine sediments (Berkman et al. 1998; Bially and MacIsaac 2000; Haltuch et al. 2000). Distributions vary not only spatially across individual lakes, but also with depth (Garton and Johnson 2000; Wacker and Von Elert 2003a; Mueting et al. 2010; Naddafi et al. 2010) so that any lake-wide inventory should involve all available biotopes, coupled with depth-distributional surveys.

In addition to adult surveys, important information about population size and factors affecting colonisation or settlement patterns in new lakes might arise from assessments of larval density and dynamics. The production and spatio-temporal distribution of veligers can vary in time or space (Nichols 1996), for example where minimum temperatures exceed those required to initiate spawning (Haag and Garton 1992; Claudi and Mackie 1994). Local water quality (Strayer and Smith 1993; Barnard et al. 2003), phytoplankton densities (Ram et al. 1996; Barnard et al. 2003) and hydrological or hydraulic factors can also affect veliger survival, transport and settlement (Griffiths et al. 1991; Barnard et al. 2003), though few assessments of any of these effects have ever made in new, artificial lakes.

One of the most high-profile, European examples of new lake creation is Cardiff Bay, formed in 2001 by the construction of a barrage across former inter-tidal mudflats in the estuaries of the Taff-Ely estuary in urban South Wales, U.K. (Cardiff Harbour Authority 2003). Although developed for amenity and as a focus for urban regeneration, the resulting 200 ha freshwater lake has been affected by several challenges including fly nuisance problems, impaired water quality and the need to maintain oxygen concentrations by continuous aeration. The lake has also been invaded since closure not only by zebra mussels, but also by a second problem species of Ponto-Caspian origin, the crustacean *Dikerogammarus villosus.*

Here, we assess the extent of zebra mussel colonisation of Cardiff Bay shortly after its formation by assessing the distribution and density of adults as well as the spatio-temporal distribution and settlement of veligers. We test three hypotheses: i) adults have preferentially colonised hard surfaces as opposed to Cardiff Bay's extensive soft sediments; ii) veliger distribution varies spatio-temporally, particularly in relation to temperature and flow conditions and iii) veliger densities determine patterns of juvenile settlement. Our broader intention is to illustrate the potential risk of disruption by invasive non-native species to the amenity and ecosystem service values new lakes exemplified here by Cardiff Bay (Limburg et al. 2010; Rothlisberger et al. 2012).

Materials and methods

Study site

Cardiff Bay (51º27′18.9706″N; 03º10′05.5186″W) was created in 2001 by the construction of a barrage across the formerly tidal estuaries of the Taff and Ely to provide an urban amenity and stimulate economic growth. Almost two-thirds of 18 million tourists who visit Cardiff annually come specifically to the lake for water sports and lakeside recreation.

Cardiff Bay has been described previously (Vaughan et al. 2008; Jüttner et al. 2009) and comprises a 200 ha freshwater lake of mean depth 4 m (maximum 13.4 m) that is isolated by Cardiff Bay Barrage from the tidal Severn estuary. Navigable locks permit boat passage, but any seawater entering the lake collects in an associated sump so that the Bay is kept close to a mean salinity of 0.19 PSU. Two nutrient-rich rivers, the Taff and Ely, discharge into the Bay from the urban and formerly industrial South Wales valleys. Median concentrations for Ammonia are 0.09 mg L^{-1} (inter-quartile range = 0.05–0.18 mg L^{-1}), for nitrate 1.33 mg L^{-1} (1.08–1.56 mg L^{-1}) and for orthophosphate 0.08 mg L^{-1} (0.04–0.11 mg L^{-1}). Although biochemical oxygen demand in the water column is low, there is some oxygen demand from the Bay's fine sediments and the Cardiff Bay Barrage Act of 1993 requires that dissolved oxygen concentrations are maintained at > 5 mg L^{-1} mostly to allow the passage of migratory salmonids. A bay-wide aeration system of 800 diffusers has been installed across the lake bed for this purpose and is connected by a series of steel-reinforced rubber pipelines thorough which compressed air is pumped continuously to enhance water-column mixing. The lake bed is mostly composed of organically enriched mud and silt, but the lake margins of 8–9 km comprise hard substrates such as harbour walls, concrete and semi-cemented or loose pebbles (Figure 1).

Adult population survey

We used a range of methods to assess the density of zebra mussels on different substrate types (Figure 1).

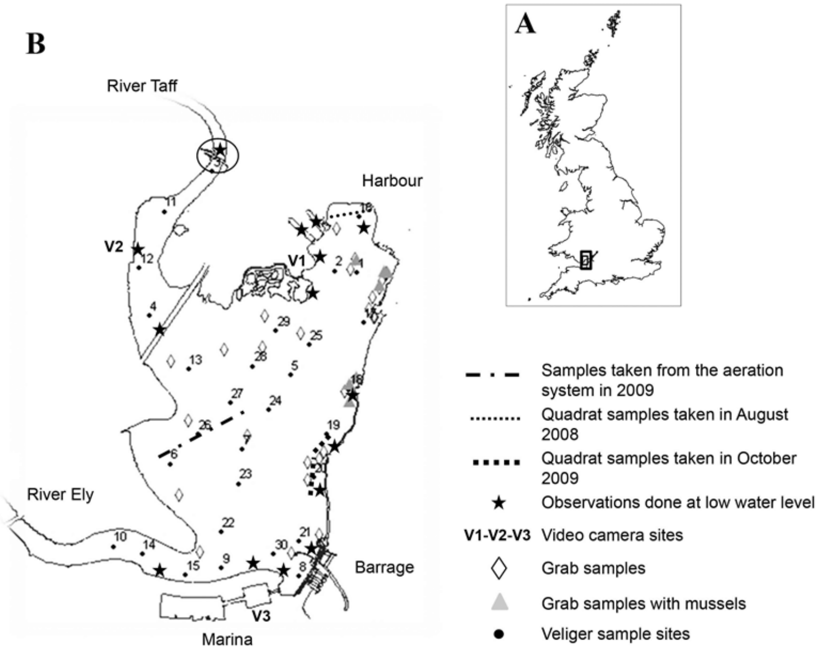

Figure 1. A. The location of Cardiff Bay in the United Kingdom. **B.** Sites in Cardiff Bay where zebra mussel density was assessed using different techniques. The encircled site corresponds to the most upstream sampling point.

For the lake bed, we used Side Scan Sonar (SSS) imaging coupled with grab samples to ground-truth any areas of apparent reef formation (Coakley et al. 1997; Sauriau et al. 1997). The SSS system, model CM2 (C-MAX.Ltd, Dorset, UK), comprised a towfish, tow cable, processing and display device, and a global positioning system (GPS). The towfish transmitted acoustic pulses (350 kHz) at right angles to the moving boat (2.5 knots) that were reflected weakly by soft sediments and strongly by hard substrates (Haltuch et al. 2000). Two surveys in November 2007 provided North East to South West parallel transects through the entire lake as well as transects in the mouths of the Taff and Ely rivers. The lake aeration system was disabled during surveys to prevent the diffusers from inhibiting effective pulse transmission. Different substrates were imaged subsequently using Multiviewer, part of the SSS processing toolkit, highlighted in ArcGis 9.2 (ESRI 2004). Any possible mussel-bed formations were then investigated using a 2L Peterson grab sampler of mouth area 270 cm^2. Thirty-four samples were taken on 9th July 2008 and the samples sorted into a white collecting basin (Figure 1). Any mussels found were preserved in ice prior to counting and measurement in the laboratory.

On three representative sections of the Bay's underwater walls, zebra mussel density, distribution and occupancy were recorded in November 2009 along vertical transects using an underwater video system (ROVTECH Systems Colour U/W): in the main Bay (site V1), in the mouth of the Taff (V2) and in Penarth Marina (site V3; Figure 1). The camera, connected to a remote-control pan and tilt unit, was mounted on a steel frame set at 22 cm from the vertical surface after first calibrating area coverage using graduated paper (1 mm) imaged from the same distance. Continual illumination was provided by two halogen lights fixed respectively on the top of the camera and on the frame, with lighting and movements controlled via a surface monitor. A calibrated rope attached to the frame recorded camera depth and, at each of the three sites, three depth-transects were chosen randomly and images recorded from the water surface to the bed at 50 cm intervals. The larger area around each transect was imaged by panning the camera to the right and the left to assess the constancy of zebra mussel cover. Video data were viewed subsequently and screen images at each depth step were used to count mussels over the 16 × 16 cm surface unaffected by edge distortion.

Where loose pebbles formed the Lake's shores, locations were accessible from land and ten randomly distributed quadrats (24 × 24 cm) were counted for mussels in these two areas (Inner Harbour and an area east of the barrage) respectively in August 2008 and October 2009 (Figure 1). All mussels were placed in bags and preserved on ice for further analysis. In addition to this detailed recording, walk-over surveys across the perimeter of Cardiff Bay were used to appraise the extent of overall colonisation. The lake's water level was intentionally dropped by 0.5 m for this purpose on August 3 2009 and the presence/absence of mussels recorded at 15 accessible points (Figure 1). We recognise the limitations of our sample sizes taken from all Cardiff Bay's habitats, but bracket our ultimate population estimate of zebra mussels widely.

Veliger survey

Veligers were sampled extensively during 2006–2009 at ten sites chosen to represent the range of environmental conditions present in Cardiff Bay (Figure 1); four sites (3, 4, 9 and 10) were in the mouths of the Taff and Ely, two in the harbour (sites 1 and 2), two in open water (sites 5 and 7), one by the west bank (site 6) and one adjacent to the barrage (site 8). Samples were collected from a boat approximately fortnightly throughout 2006 and 2007, and from May to October during 2008 and 2009, using a conical plankton net with fine mesh (60 µm) and mouth diameter 20 cm. The net was hauled from the bed to the surface thereby sampling the entire water column. Plankton samples were preserved on-site in 70% IMS and veligers sorted and counted at 40× magnification. Samples with high veliger densities (>200 per sample) were sub-sampled. By calculating the volume of water sampled, veliger density could be expressed as number per litre. In September 2006 and September 2007, we assessed spatial distribution more intensively at 30 sites through the lake using identical methods (Figure 1).

Water quality

Contemporaneously with veliger sampling (i.e. fortnightly), water samples were collected at each site to assess the total concentration ($\mu g.l^{-1}$) of chlorophyll *a* using fluorimetry (model bbe Moldaenke, Germany). Surface temperature, dissolved oxygen, turbidity, pH, conductance and salinity were measured using a model 6920 sonde (YSI Inc., USA) on each sampling occasion as part of a continuous monitoring programme operated by Cardiff Harbour Authority since Cardiff Bay was formed in 2001.

Discharge rates in the Rivers Ely and Taff were recorded every 15 minutes at gauging stations operated by Natural Resources Wales respectively at St Fagans (Easting 312099, Northing 177312) and Pontypridd (Easting 307908, Northing 189585). River discharge into Cardiff Bay was then estimated by combining these two river flows. Because of the logistical challenges involved, variations in current velocity across Cardiff Bay were assessed only once during this study, in February 2008. Local velocity was measured every five seconds along a series of transects across Cardiff Bay water using a 1500kHz frequency Acoustic Doppler Current Profiler (Sontek, USA) linked into a laptop running Coastal Surveyor software (Sontek, USA). Current velocity data were then interpolated using ArcGIS (ESRI 2004).

Veliger settlement

Patterns of veliger settlement were assessed experimentally using artificial substrates in 2007, 2008 and 2009. Plastic crates (60 cm length × 40 cm width × 28 cm height), each containing two × three replicate substrates of clay tiles, pebbles and steel were deployed on the lake bed at 4–6 metres depth during the veliger production period from early June to late September at each of the veliger sampling sites (sites 1–10; see Figure 1). Each was attached to a surface buoy or one of Cardfif Bay's wooden piers (known locally as "dolphins"). The tiles (15 × 1.3 cm) were chosen to resemble hard surfaces in Cardiff Bay. Ovoid pebbles (6 cm length × 4 cm diameter), fixed into inert epoxy resin (Horvath and Lamberti 1999) represented the Bay's pebble substrates and stainless-steel tubes (12 cm length × 5 cm diameter) were taken to represent sections of the Bay aeration system. Substrates were positioned randomly in the crates.

Upon collection, artificial substrates were detached, sealed in plastic bags and transported in a cool box to the laboratory. Visible juvenile mussels were then removed, counted and preserved in 70% alcohol. Dimensions of the tiles and steel tubes were measured and surface areas calculated. For pebble substrates, this involved wrapping each in aluminium foil to calculate the area of foil required to attain coverage (Mackie 1993). In all cases, juvenile settlement was then expressed as number of individuals per metre square.

Heavy silt deposition onto the artificial substrates during the first experiment in 2007 led to a change in design in which substrates were oriented vertically in 2008 and 2009 rather than horizontally. This does not affect mussel settlement (Czarnoleski et al. 2004; Kobak 2005) and in any case vertical orientation matched that of most occupied surfaces in Cardiff Bay. Despite losing artificial substrates to sedimentation effects in 2007, we removed and counted juveniles from the lateral crate surfaces in six randomly located quadrats (10 × 10 cm). Similar data were then collected in 2008 using identical methods in addition to the artificial substrate samples.

Statistical analyses

Hypothesis i): adult mussels. To estimate variation in adult mussels among locations on vertical surfaces, we used analysis of variance using PROC GLM procedure of SAS accounting for site and depth effects (SAS Institute Inc. 1999). Transects were treated as random factors nested within sites. Where sites or depths differed ($P < 0.05$), least squares means were derived using the PDMIX800 macro (Saxton 1998).

After reviewing results from the Bay's fine sediments (see below), the total zebra mussel population in Cardiff Bay was estimated crudely by considering only the two main habitats in the lake's shoreline: vertical surfaces (including the barrage) and the pebble banks. This ignored the aeration system and other infrastructure in the Bay that also supports mussels, such as pontoons, so our estimate should be considered as conservative. The perimeter length of each major habitat was estimated using ArcGIS and area derived by multiplying perimeter measurements by the mean depth as determined from the average of all transects (3.5 m). The depth range of the pebble banks was estimated at 3 m based the Bay's structure prior to inundation. Total population could then be assessed from total habitat area and local mussel densities, accounting for error variation.

Hypothesis ii): spatio-temporal variation among veligers. Prior to any use in veliger analysis, environmental variables (river discharge, chlorophyll *a* concentration etc) were transformed using log, square root or exponential functions to minimise kurtosis and skewness, and to ensure homogeneity of variance. Some comparisons among years required that veliger densities were standardised within years by subtraction of the mean and division by the standard deviation. This procedure allowed an expression of standard veliger densities across sites and months relative to the annual mean.

To characterise conditions under which veligers were produced, water temperature, river discharge and chlorophyll *a* concentration were compared between non-spawning (November–March) and spawning periods (April–October) using one way ANOVA. Seasonal and temporal variations in veliger density were assessed using pooled data from sites 1, 2, 5, 6, 7, 8, 9 and 10 from which means were calculated for each sampling date. Sites 3 and 4 were excluded because veliger densities here were effectively zero. Variations in environmental conditions and veliger density between years (2006, 2007, 2008 and 2009) and months were assessed using Generalised Linear Modelling (GLM) procedures in R with either a Gaussian error distribution, identity link function (veligers) or other appropriate error terms for water temperature, discharge, chlorophyll *a* concentration, salinity, turbidity, pH and dissolved oxygen.

To assess how veliger density tracked conditions through the four year study, we related numbers to environmental variations by reducing these to major variates using principal components analysis (PCA) on water temperature, discharge, chlorophyll *a* concentration, salinity, turbidity, pH and DO. Veliger densities were plotted against Principal Component axes and Pearson's correlation coefficient calculated.

Variations in veliger density across the 30 sites in the detailed spatial survey were assessed by mapping spatial patterns in ArcGIS (ESRI 2004) using spline interpolation, which interpolates values for cells in a raster from a more limited number of sample data points. Correlation was used to relate local veliger densities to environmental conditions at each site parameterised as variates from principal components of water temperature, chlorophyll *a* concentration, salinity, turbidity, pH and dissolved oxygen.

Hypothesis iii): veliger settlement. Variations in veliger settlement between 2007 and 2008 on the crate surfaces only were assessed using a Kruskal-Wallis test (K-W). More extensive spatial variations in veliger settlement were examined first by mapping spatial patterns at the 10 sites using ArcGIS (ESRI 2004), focussing on the years with the highest densities (2007 and 2009). Linear Pearson correlations between juvenile settlements among sites across years were also calculated to assess whether spatial patterns were preserved through time. Finally, the relationship between juvenile settlement on crates (2007, 2008) or artificial substrates (2008, 2009) were analysed using regression against mean veliger density per location.

To assess the more local effects of artificial substrate on veliger settlement, we used ANOVA with Generalised Linear Mixed Modelling (GLMM) using R on settled juvenile density from the two years unaffected by sedimentation (2008 and 2009) and after log transformation. These analyses simultaneously assessed variations between years and crate depths using a residual maximum likelihood (REML) linear mixed model. Site was defined as a random term and significances were tested using the Wald statistic, which is distributed as chi-square.

Results

Adult density and distribution

Side Scan Sonar showed that soft sediments were largely free of zebra mussels, occurring in only 7 of 34

Table 1. Variations in the density of zebra mussels along replicate depth profiles from 0.5–2m as shown video images at different sites in Cardiff Bay. P-values are obtained by REML linear mixed model, with alpha set at 0.05 as the significant level. Superscripts indicate depths or sites which were significantly different from others.

	Mussel density mean	SE	N	Overall F (P)
Depth (m)				
0.5^1	451	181	11	$F_{3,21}$=27.13 (P < 0.001)
1	1360	181	11	
1.5	1570	178	10	
2	1685	389	7	
Sites				
Marina^1	693	127	15	$F_{2,8}$=16.04 (P<0.002)
St Davids' Hotel	1541	217	16	
River Taff	1619	220	9	

grab samples and at two locations (2700 ± 1900 m^{-2} to 3300 ± 1200 m^{-2} SE; Figure 1). High coefficients of variation indicated marked patchiness in both cases (76% and 118%).

By contrast zebra mussels occurred on all hard substrates at depths of 0.5–7 m, including the barrage infrastructure, and in the mouths of both the Ely and Taff rivers with the exception of the most upstream site (Easting 318549.9, Northing 174584.3; Figure 1). Densities on pebbles ranged from 950 ± 250 m^{-2} (SE) to 3700 ± 370 m^{-2} (SE; CV = 10%–26%), while video surveys showed ubiquitous cover on vertical walls and hard surfaces at densities increasing with depth from c 450 m^{-2} at 0.5 m to over 1600 m^{-2} at 1–2 m (Table 1). Mean densities varied between sites, being lower in the Marina (700 ± 130 m^{-2} SE) than in either the main Bay (1550 ± 220 m^{-2} SE) or in the River Taff (1600 ± 220 m^{-2} ± SE) (Table 1).

The vertical surfaces and pebble habitats on which zebra mussels were abundant covered c 4500 and 3900 m respectively of the Cardiff Bay perimeter, or areas of 13500 and 7800 m^2 after accounting for the absence of mussels at depths < 0.5m. Multiplying these areas by the lowest and highest possible densities of zebra mussels from the ranges recorded suggested a likely total population of 9.5 to 30.5 million individuals with a likely live biomass of 9–29.4 tonnes.

Veliger distribution through time

Veligers occurred from late May until October (Figure 2), when water temperature (ANOVA, $F_{1,70}$ = 160.9, P < 0.001) and chlorophyll *a* ($F_{1,65}$ = 61.3, P < 0.001) were elevated and discharge was low (ANOVA, $F_{1,70}$ = 22.8, P < 0.001). Veligers appeared at water temperature > 14 °C and peaks in larval density thereafter coincided temperatures of 17–21 °C (Figure 2). Averaged over all years, spawning activity was greater in June (8.4 ± 1.9 l^{-1} to 14.1 ± 4 l^{-1} (SE) depending on year) than in May (t_{36} = 3.23, P = 0.003), July (t_{36} = 2.32, P = 0.03), August (t_{36} = 2.49, P = 0.02) or September (t_{36} = 2.75, P = 0.01; Tables 2 and 3). Peak spawning coincided with the lowest river discharge (10.1 ± 1.8 $m^3.s^{-1}$).

Environmental conditions in Cardiff Bay varied between years with apparent consequences for veliger production and/or retention (Tables 2 and 3). After accounting for variation between months, the Bay was significantly warmer in 2006 (18.9 ± 0.9 °C) than in 2007 (16.5 ± 0.6 °C, t_{130} = 6.1, P < 0.001), 2008 (16.2 ± 0.7 °C, t_{130} = 7.1, P < 0.001) or 2009 (16.8 ± 0.7 °C, t_{130} = 6.4, P < 0.001; Tables 2 and 3). Mean river discharge was significantly greater in 2008 than 2006 by 3×, 2009 by 2× and 2007 by 1.8× (Tables 2 and 3). Salinity was significantly greater in 2006 than in 2008 (t_{36} = −3.59, P = 0.001) and 2009 (t_{36} = −3.61, P = 0.001), but not in 2007 (t_{36} = −1.71, P = 0.1) probably reflecting dilution. These inter-annual variations were tracked by changes in veliger densities, which were significantly higher by almost 3–4× in the drier 2006 than in 2008 (t_{36} = −2.7, P = 0.01) and significantly higher also than in 2009 (t_{36} = −2.4, P = 0.03) (Figure 2; Table 2). Judged over all months and years, veliger density increased significantly (r = 0.59, P < 0.001; Figure 3) along a variate derived from principal components analysis that reflected increased water temperatures, high chlorophyll *a* concentration and low river discharge.

Veliger distribution

Discharge in the river Taff was four times greater than the Ely (M-W test, n = 15, P < 0.001) and the former Taff channel through Cardiff Bay appeared to have the greatest current velocity (Figure 4c).

Values for several determinands were lower in the river mouths than in the main Bay, except for DO, while temperatures (16.3 v 17–18.3 °C) and DO (8–8.4 v 11 $mg.l^{-1}$) were also higher in the Taff than the Ely. These variations were captured by Principal Component Analyses of physic-chemical conditions

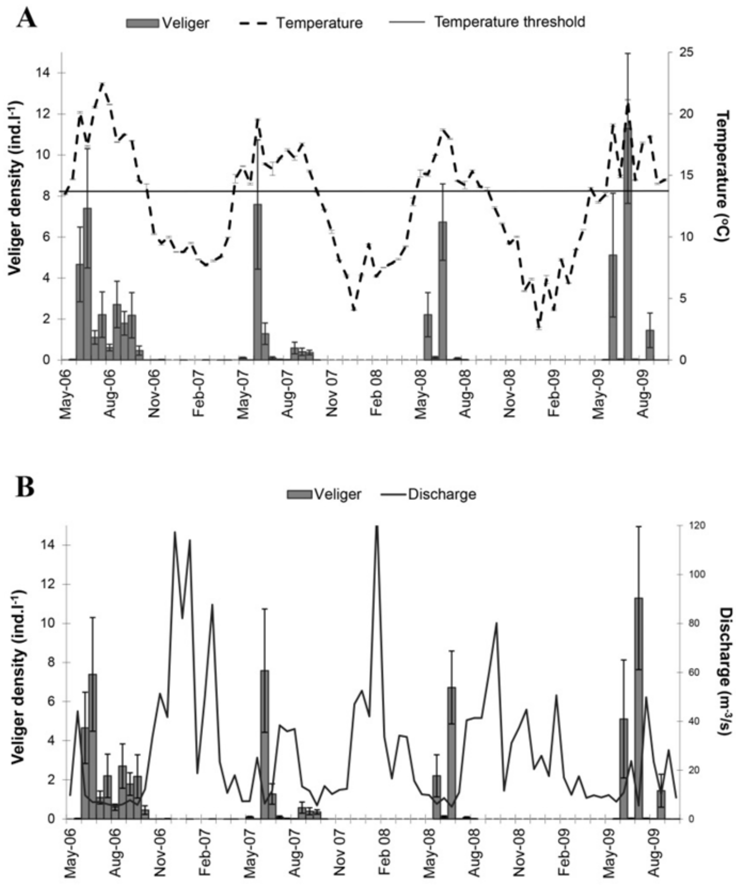

Figure 2. Variations in the density of zebra mussel veligers in Cardiff Bay over the four-year study-period (bars) showing also (**A**) water temperature variations and apparent threshold for reproduction and (**B**) variations in discharge in the two major rivers draining into Cardiff Bay. Bars are standard errors.

at the 30 sites sampled in September 2006 and September 2007 to which spatial patterns in veliger numbers could be related. Veligers were most numerous in similar areas of the Bay in both these years ($r = 0.49$, $P = 0.01$; (Figure 4a, b), mostly areas with low scores on PC1, to which veliger numbers were significantly negatively correlated in both 2006 ($r = -0.51$, $P = 0.007$) and 2007 ($r = -0.44$, $P = 0.02$). In other words, veligers were most numerous in warmer waters rich in chlorophyll *a* and lower in DO than elsewhere.

Veliger settlement

On the crates containing artificial substrates, juvenile density was significantly higher in 2007 (32800 m^{-2} ± 3000 SE) than 2008 by over 120 times (270 ± 70 m^{-2}; M-W test, $W = 3296$, $P < 0.001$; Figure 5a), reaching a maximum density of 54700 ± 700m^{-2}. Settled juvenile densities were inter-correlated between 2007 and 2008 across sites ($r = 0.74$, $P = 0.06$, Figure 5b) implying some consistency in the spatial pattern of colonisation across years (Figure 6). This effect appeared to be mediated by veliger numbers, and in both 2007 and 2009 (on artificial substrates), settlement was significantly higher where veliger densities in the water column were greatest (2009: $F_{1,6} = 14.45$, $P = 0.009$; 2007: $F_{1.7} = 4.31$, $P = 0.08$; Figure 7).

Juvenile densities were significantly higher in 2009 than in 2008 on all artificial substrates (Table 4). On pebbles, average values in 2009 (7200 ± 2400 m^{-2}) exceeded those in 2008 (300 ± 100 m^{-2}) by 24 times ($F_{1,80} = 8.130$, $P < 0.001$). Juvenile densities on tiles were 3600 ± 1000 m^{-2} in 2009 and 400 ± 100 m^{-2} in 2008, and on steel 1300 ± 500 m^{-2} in 2009 and 300 ± 500 m^{-2} in 2008. Substrate depth had no effect on juvenile settlement (Table 4). Having accounted for variations among years, juvenile settlement varied significantly between artificial substrate types ($F_{2,80} = 8.130$, $P < 0.001$; Table 4), with juvenile density on pebbles and tiles roughly twice that on steel substrates.

Table 2. Variations among years and months in environmental measures and zebra mussel veliger densities in Cardiff Bay during the reproductive season. The values are means (with SE) for each year or month and significant differences are indicated by differing superscripts (see Table 3 for statistical analysis).

	Veliger density (ind.l^{-1})	Temperature (°C)	Discharge (m^3.s^{-1})	Chlorophyll *a* (µg.l^{-1})	Salinity (PSU)
Year data mean					
2006	3.1 ± 0.9 ^{a}	18.9 ± 0.9 ^{a}	10.9 ± 4.2 ^{a}	7.9 ± 1.5	0.22 ± 0.01 ^{a}
2007	1.3 ± 0.9 ^{ab}	16.5 ± 0.6 ^{b}	19.2 ± 4.3 ^{b}	6.6 ± 2.6	0.19 ± 0.01 ^{ab}
2008	1.2 ± 1.2 ^{b}	16.2 ± 0.7 ^{b}	35.2 ± 10.8 ^{c}	6.2 ± 1.3	0.15 ± 0.02 ^{b}
2009	1.9 ± 1.2 ^{b}	16.8 ± 0.7 ^{b}	16.9 ± 4.0 ^{b}	6.1 ± 1.3	0.16 ± 0.01 ^{b}
Month data mean					
May	0.04 ± 0.03 ^{b}	13.9 ± 0.5 ^{a}	20.9 ± 8.8 ^{a}	4.3 ± 1.7	0.17 ± 0.02 ^{b}
June	4.6 ± 1.4 ^{a}	17.9 ± 0.7 ^{b}	10.1 ± 1.8 ^{b}	10.5 ± 2.7	0.18 ± 0.01 ^{a}
July	1.9 ± 1.4 ^{b}	18.0 ± 0.9 ^{c}	22.7 ± 6.0 ^{a}	5.5 ± 1.3	0.17 ± 0.01 ^{b}
August	1.0 ± 0.6 ^{b}	17.8 ± 0.7 ^{b}	19.5 ± 5.6 ^{a}	7.0 ± 1.6	0.19 ± 0.02 ^{b}
September	1.0 ± 0.5 ^{b}	16.1 ± 0.6 ^{d}	26.0 ± 10.1 ^{c}	4.6 ± 1.7	0.19 ± 0.02 ^{b}

Table 3. Generalised Linear Model analysis of variations in environmental data and veliger data between months and years for Cardiff Bay. Bold typeface indicates a significant difference of the variables between 2006, 2007, 2008 and 2009, and a significant difference between May, June, July, August, September. The diverse error distributions and link functions used for each variable analysis are indicated.

	Difference between years	Difference between months	Error distribution and link function
Temperature (°C)	**$F_{3,130}$ = 25.7 P < 0.001**	**$F_{4,130}$ = 19.8 P < 0.001**	Gaussian – Inverse
Discharge (m^{-3}.s^{-1})	**F3,603 = 25.3 P < 0.001**	**F4,603 = 12.6 P < 0.001**	Gaussian – Log
Chlorophyll a (µg.l^{-1})	F3,36 = 0.55 P = 0.65	F4,36 = 1.44 P = 0.25	Gaussian – Log
Salinity (‰)	**F3,36 = 18.18 P < 0.001**	F4,36 = 1.68 P = 0.79	Gaussian – Identity
DO (mg.l^{-1})	F3,36 = 0.62 P = 0.61	F4,36 = 0.87 P = 0.49	Gaussian – Log
Turbidity (NTU)	F3,36 = 1.32 P = 0.29	F4,36 = 0.85 P = 0.51	Inverse Gaussian – Identity
pH	F3,36 = 2.3 P = 0.10	F4,36 = 1.7 P = 0.17	Gaussian – Identity
Veliger (ind.l^{-1})	**F3,36 = 2.97 P = 0.048**	**F4,36 = 3.50 P = 0.02**	Gaussian – Identity

Discussion

These data show that at least 9–31 million zebra mussels had established in Cardiff Bay within 5–8 years following impoundment in 2001. Population age structure reported by Alix (2010) showed that an adult cohort of mussels was already present in Cardiff Bay in 2005, implying that spawning mussels must have been there by 2004 and that that colonisation had occurred by 2003. We know of few previous lake-wide inventories of this invasive non-native species and none from a newly formed lake. All three of the hypotheses tested were supported. With respect to hypothesis (i), zebra mussels were scarce on the Bay's extensive soft sediments, but occurred extensively across all the Bay's hard surfaces. With respect to hypothesis ii) veligers were abundant in the water column at 8–14 individuals L^{-1} during peak periods of spawning, and accumulated particularly under warmer, low-flow conditions and in locations characterised by the greatest concentrations of chlorophyll *a*. Finally, supporting hypothesis (iii), high veliger densities led to the highest rates of colonisation of artificial hard substrates—at least in drier years. The general implication is that new lakes—including those designed specifically for amenity such as Cardiff Bay—are at risk of extensive occupation by zebra mussels or other aquatic, invasive, non-native species. The potential ecological effects of invasive species on amenity values and ecosystem services should therefore be considered in scenarios and risk assessments when new lakes are planned. We discuss these themes on more detail below.

Adult population estimate

Confidence in our overall population estimate for zebra mussels in Cardiff Bay depends on measurements of density from contrasting methods as well as accurate assessment of habitat availability and occupancy across the Bay. While peak zebra mussel densities can reach 60,000–115,000 m^{-2} locally (Cleven and Frenzel 1993; Mackie and Schloesser 1996), the mean densities we recorded (450–5100 m^{-2}; up to 7700 m^{-2} on the aeration system) were closer to

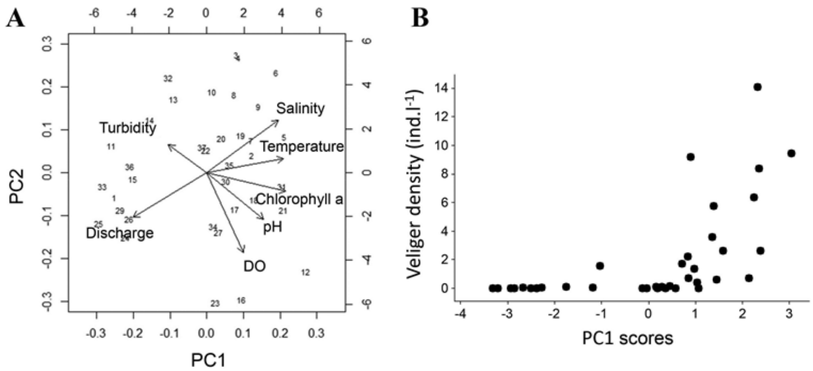

Figure 3. A. Two-dimensional ordination using principal components analysis of the environmental variables recorded in Cardiff Bay during veliger production (May–September) over the four year study period (2006–2009). **B.** Variations in the density of zebra mussel veligers in Cardiff Bay plotted against PC1.

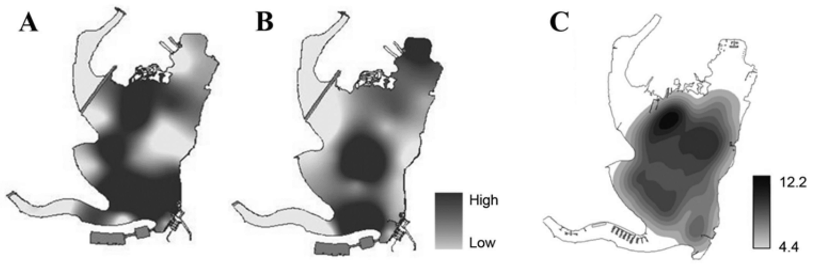

Figure 4. A, B. Veliger densities across Cardiff Bay interpolated from data recorded at 30 sites in September 2006 and September 2007. **C.** Current velocity values (cm.s^{-1}) recorded in February 2008 and interpolated through Cardiff Bay.

those from other European lakes in Ireland (3900 m^{-2}; Lucy 2005), Poland (1500 m – 4700 m^{-2}; Burlakova et al. 2000) and Finland (2200 ± 800 m^{-2}; Orlova and Panov 2004) suggesting that our data are within ranges observed elsewhere. Once established, Cardiff Bay's eutrophic, temperate character would be expected to provide conditions conducive to zebra mussel recruitment and growth (Nalepa et al. 1995; McMahon 1996; Jantz and Neumann 1998; Karatayev et al. 1998).

Additionally, the distribution of habitats occupied by zebra mussels in Cardiff Bay matches the patterns elsewhere. The Bay's extensive soft, benthic sediments were avoided by zebra mussels except for modest development in patches. Elsewhere, for example in Lake Erie, mussel aggregations have developed over soft substrates, for example on reefs of woody debris and dead mussel shells (Coakley et al. 1997; Berkman et al. 1998, 2000), but this requires physical conditions that permit veliger settlement (Bially and MacIsaac 2000). Moreover, in Lake Erie aggregations on soft sediment are largely of quagga mussels *Dreissena bugensis* (Mills et al. 1996), which have not yet colonised Cardiff Bay after arriving only in the UK in 2014. Additionally, in Cardiff Bay, conditions are apparently unsuitable for zebra mussels over soft sediments and our colonisation experiments illustrated how rates of sediment deposition were rapid enough to prevent juvenile mussel settlement on horizontal surfaces. In contrast, zebra mussels have colonised most hard substrates in Cardiff Bay including the aeration system, the marginal areas of pebbles and cobbles, and any vertical or sloping hard surfaces that are clear of fine sediment deposition.

Table 4. Minimal restricted maximum likelihood (REML) modelling showing how the settlement of juvenile zebra mussels varied among years, substrates and depth in Cardiff Bay (random terms = sites).

Model term	Wald statistic (χ^2)	d.f	*P*
Artificial substrate	7.12	2, 62.4	0.002
Year	27.56	1, 63.6	<0.001
Depth	0.89	1, 46.1	0.35

Although there was a lack of depth effects overall on juvenile settlement (Table 4), there was some evidence that zebra mussel densities on occupied surfaces was restricted in shallow water. Individuals were absent up to 0.5 metres from the water surface, but increased to a maximum density between 1–2 m which then persisted to depths of 3–7 m. Kobak (2000) has shown from laboratory studies that zebra mussels avoid locations directly illuminated and where there are UV effects (Seaver et al. 2009), though depth distribution might also reflect cues to prevent risks of water-level fluctuation at the surface. Wave action

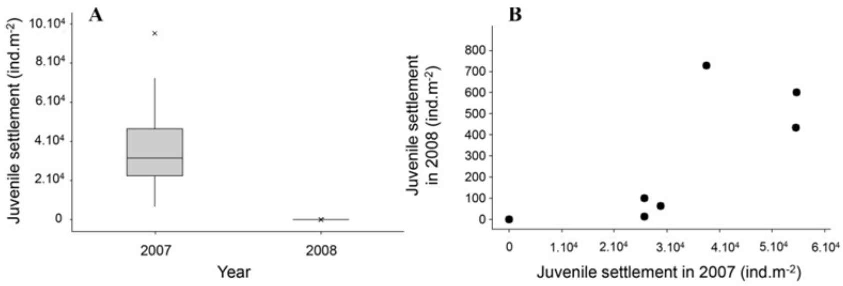

Figure 5. Juvenile settlement densities on crates deployed in Cardiff Bay over the summer periods of 2007 and 2008. **A.** Box-plots of juvenile settlement (ind.m^{-2}) on plastic crates at sites 1, 2, 4, 5, 6, 8 and 9 in 2007 (n = 52) and 2008 (n = 41; K-W test *** P < 0.001) **B.** Correlation between juvenile settlement in 2007 and 2008 among locations.

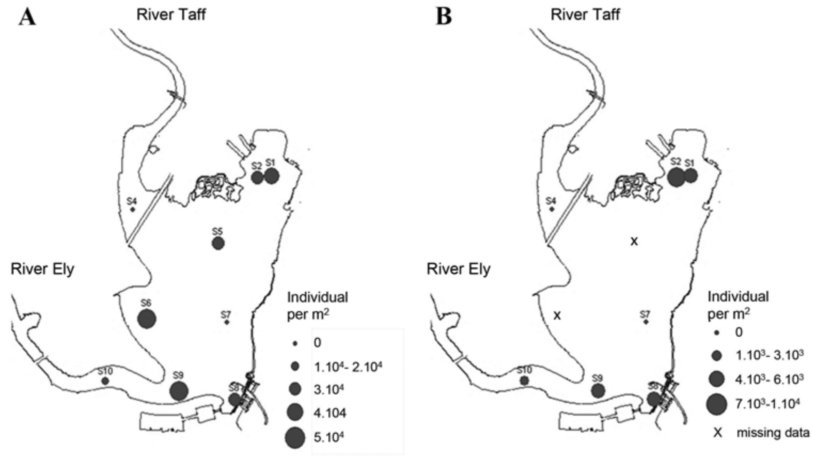

Figure 6. Settlement of zebra mussels at different experimental sites in Cardiff Bay: **A.** densities estimated from quadrat samples collected on plastic crates in 2007; **B.** densities estimated from artificial substrate in 2009.

also inhibits mussel settlement and such effects are liable to greatest in shallow waters (Chase and Baley 1999; Kobak 2005). Zebra mussel densities at 1–5 m reflect optimum distribution with respect to temperature, oxygen concentration and planktonic food production (Mellina and Rasmussen 1994; Karatayev et al. 1998). These depth-related effects and other aspects of heterogeneity in zebra mussel distribution in Cardiff Bay complicated our overall population estimate of 9–31 million adult individuals and live biomass of 9–29.4 tonnes. Moreover, this estimate required the use of different sampling methods in the Bay's heterogeneous set of biotopes each with their own potential errors. Because of the resulting uncertainties, our total population estimate requires some caution, but we made it conservatively using a bracketing procedure based on the lowest and highest possible local densities rather than on a mean density weighted by depth or habitat type. In support, the estimate of zebra mussels present on Cardiff Bay barrage alone of 2.4–5.5 million individuals, or 2.3–5.2 tones, corresponded closely to the value of the mussel biomass actually removed during maintenance from this structure of around 4 tonnes (Cardiff Harbour Authority, unpublished data).

Veliger density, dynamics and distribution

At 8–14 individuals per litre, the density and dynamics of zebra mussel larvae provided further evidence of the extent to which Cardiff Bay was quickly occupied by zebra mussels: during peak reproduction and reduced summer discharge, veligers contribute up to 20% of the Bay's total animal plankton as one of the most abundant components (Merrix-Jones et al., unpubl. data). Based on a crude estimate of lake volume (200 Ha and mean depth 4 m), at peak density Cardiff Bay must contain c 11×10^{10} veligers, or c 3,700–12,400 per adult mussel present. Accurate modelling of total veliger output would require adjustment to account for the Bay's flushing rates (55 to > 220 h, see below) as well as changing veliger production through the season, but these values are consistent with a large reproducing population. The absolute veliger densities recorded were within the range of maxima recorded elsewhere in occupied American and European lakes of 7–700 ind.l^{-1} (Sprung 1995), although values vary through the colonisation sequence as well as with environmental conditions. For example, in Lough Key

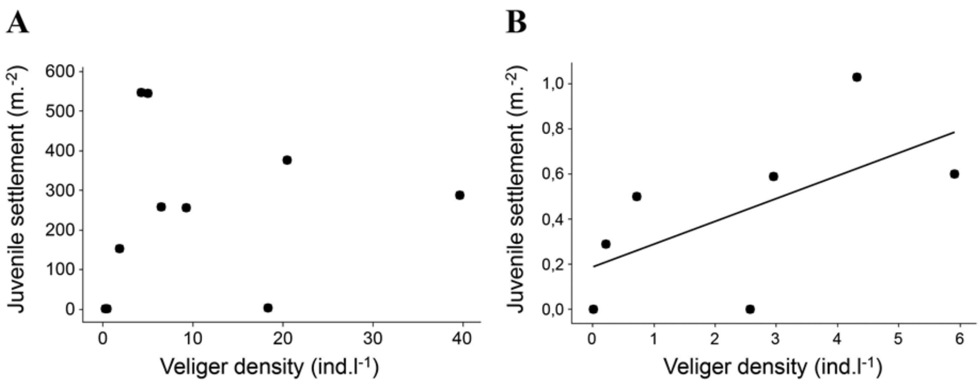

Figure 7. The relationship between the settlement of zebra mussel juveniles and the abundance of veligers at sites in Cardiff Bay in two contrasting years. Only years with significant relationships are shown: **A**. Juvenile settlement estimated from crate samples taken at sites 1, 2, 4, 5, 6, 8, 9 and 10, in 2007 ($F_{1,7}$ = 4.31); **B**. Juvenile settlement estimated from artificial substrates at sites 1, 2, 4, 8, 9, 10 and 11, in 2009 ($F_{1,6}$ = 14.45). **Note:** In 2008, juvenile settlements estimated from crate samples taken at sites 1, 2, 5, 6, 8 and 9, and from artificial substrates at sites 1, 2, 4, 5, 6, 8, 9 and 10, were not significantly correlated to veliger density, respectively (P = 0.17; $F_{1,5}$ = 2.51), (P = 0.994; $F_{1,7}$ = 0.00).

(Ireland) veliger densities were 3–20 ind.l^{-1} in the early stages of occupancy, but reached densities of 39–45 ind.l^{-1} within three years (Lucy 2005). In the Muggelsee, Germany, densities ranged from 43–160 ind.l^{-1} with prevailing climatic conditions linked to temperature, stratification and reduced oxygen concentrations (Wilhelm and Adrian 2007).

The Cardiff Bay data also reveal how climatic conditions influence veliger densities both within and between years through spawning activity as well as through residence times and retention. The seasonality of zebra mussel reproduction varies over its invasive range and is influenced by environmental conditions (Nichols 1996). Reproduction in Cardiff Bay lasted from May to September/October, synchronous with peak phytoplankton production (Figure 3 and Merrix-Jones et al., unpubl.) and the threshold temperature to initiate larval production was apparently 14 °C. Elsewhere, 12 °C is the lowest likely threshold for zebra mussel reproduction, though values range up to 19 °C (Sprung 1995; Claudi and Mackie 1994; Nichols 1996; Karatayev et al. 1998; Lucy 2005) possibly because planktonic food supplies also influence reproduction through gonad volume, fecundity and reproductive investment (Wacker and von Elert 2003b; Galbraith and Vaughn 2009). Our monitoring over four years suggested some plasticity in zebra mussel spawning in Cardiff Bay, divided into 1–3 events per year (Figure 2): for three reproductive seasons, the major larval peak occurred in May/June followed by a smaller peak in August, but exact patterns varied inter-annually. Comparison across locations also shows spawning plasticity in zebra mussels from one event per year to two or three (Haag and Garton 1992; Bacchetta et al. 2001; Wilhelm and Adrian 2007). This is consistent with laboratory data showing that gamete release occurs in 2–6 events, with around half of the eggs produced during the first (Waltz 1978; Haag and Garton 1992). However, discharge also had major effects on veliger density, and during some periods of 2007 (June to early August) and 2008 (July–August), veligers were barely detectable when flow through the Bay reached 35–40 m^3 s^{-1}. Large reductions in veliger numbers also occurred in wet periods interspersed between peak larval numbers during 2009. Based on a lake area of 200 hectares and mean depth 4 m, at these discharges complete flushing of Cardiff Bay could occur in just 55–60 h, and any suspended veligers would have been lost downstream into the adjacent Severn estuary (Griffiths et al. 1991; Carlton 1993). This compares with flushing times of well over 220 h under the drier conditions at discharges < 5–10 m^3 s^{-1} when veliger numbers were maintained (Figure 2). Overall, discharge was one of the key predictors of veliger densities (Figure 3).

In addition to varying in time, veliger densities varied spatially across Cardiff Bay. For example, in the mouths of the inflowing Taff, temperature, chlorophyll *a* concentration and turbidity were all lower than in the main Bay as a result of increased current velocity that would also be likely to prevent retention and upstream movement by zebra mussel veligers (Griffiths et al. 1991; Schiemer et al. 2001).

More veligers were found in the mouth of the slower River Ely. Elsewhere in the Bay, veligers accumulated in areas with restricted river flow, high water temperatures and high chlorophyll *a* concentrations—such as the Inner Harbour, shallow areas around sites 6 and near the barrage.

Variations in veliger density in both space and time appeared to affect patterns of juvenile settlement, with years and locations with the highest veliger numbers also characterised by the greatest settled juvenile densities. Thus, artificial substrates in areas of increased veliger density had greater juvenile settlement in both 2007 and 2009 (Figure 7), while areas with the greatest juvenile settlement were consistent across years (Figure 5b). Settled densities were also considerably greater in 2007 than the wetter 2008. Veliger density affected juvenile settlement also in Lake Erie, where daily settlement rates increased with local veliger concentration (Martel et al. 1994). One implication is that reduced discharge appear to favour zebra mussel colonisation and it is interesting to speculate that zebra mussel colonisation of Cardiff Bay in 2003 would have coincided with a particularly dry, hot year. Such an effect would support predictions that colonisation by invasive non-native species may be facilitated under future climate (Kernan 2015).

Conclusions

Although a range of management problems were anticipated when Cardiff Bay was conceived as an urban amenity, they did not include the risk of colonisation by invasive non-native species (Hill et al. 1996). However, zebra mussel colonisation followed within 2–3 years of the Bay's closure in 2001 and the population has since been maintained by a combination of i) reproductive strategies that are flexible enough to support recruitment through the intra- and inter-annual environmental variation in the Bay's conditions; ii) strong propagule pressure, with veligers dispersed at high densities throughout the entire lake; iii) extensive habitat availability and iv) suitable water quality rich in nutrients, calcium, plankton and dissolved oxygen that in combination have supported population development. This combination of circumstances is likely to be reproduced in many other artificial lakes where biosecurity and the risk of colonisation by this or other non-native species should be an important consideration. In the case of Cardiff Bay specifically and despite its amenity importance, no assessment of the effects of zebra mussels on ecological processes and ecosystem services that the Bay provides has been carried out. Experience from other occupied water bodies is that large effects are likely on infrastructure, maintenance costs, nutrient cycling, phytoplankton dynamics, photosynthesis, turbidity, oxygen dynamics, habitat conditions and the dynamics of other invasive species. In Cardiff Bay, there are legal requirements to maintain oxygen concentrations using aeration, but also concerns that zebra mussels could increase oxygen uptake while indirect affecting photosynthesis by reducing phytoplankton biomass. Moreover, with larval densities and adult populations in Cardiff Bay so large, and human visits so frequent, the risk for onwards population dispersal through boats, angling and other amenity use are biosecurity considerations that the Harbour Authority must now manage.

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